Spring 2020

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Recommended Citation

Ukishima, Lindsey A., "Analysis of an ODE Model for Sea Turtle Populations with Temperature-Dependent Sex Determination" (2020). *Student Publications*. 943.
https://cupola.gettysburg.edu/student_scholarship/943

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Abstract

The sex of green sea turtles is determined by the temperature at which the eggs are incubated. Recent studies have shown that the sex ratios of sea turtle populations have changed over recent years, likely due to climate change, which has produced a more female-biased population. This paper finds the nonzero equilibrium point of the novel system developed by Herrera et a. (2019) and attempts to determine the stability of the population at that point.

Keywords

Differential equations, sex determination, modeling, temperature-dependent

Disciplines

Applied Mathematics | Environmental Sciences | Mathematics

Comments

Written for MATH 460: Individualized Study-Research

Analysis of an ODE Model for Sea Turtle Populations with Temperature-Dependent Sex Determination

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Abstract

The sex of green sea turtles is determined by the temperature at which the eggs are incubated. Recent studies have shown that the sex ratios of sea turtle populations have changed over recent years, likely due to climate change, which has produced a more female-biased population. This paper finds the nonzero equilibrium point of the novel system developed by Herrera et al. (2019) and attempts to determine the stability of the population at that point.

1 Biological Background

In many species of turtles, temperature-dependent sex determination has been observed. Temperature-dependent sex determination (TSD) is the process in which the temperature of an embryo's environment influences the production of hormones that dictate the sex of the embryo. This means that the sex of the organism is environmentally dependent, which means that it is dependent on factors in the physical and biotic environment. Turtles that exhibit TSD have a period of thermosensitivity during which the sex of the embryo is determined. For turtles, this period takes place during the mid-trimester of the embryo incubation period [2]. In TSD, there are three different patterns that species use: FM, MF, and FMF. In FM patterning, female eggs develop at lower temperatures while male eggs develop at higher temperatures; MF patterning is the inverse of FM patterning. And, FMF patterning indicates that female eggs develop at both low and high temperatures while males develop at a medium temperature range [8]. Turtles follow an MF pattern; this indicates that at lower temperatures there are mostly male hatchlings and at higher temperatures there is a mostly female hatchling population. The temperature at which the sex differentiates is around 29.4°C [12]; this temperature is called the pivotal temperature. It is at this temperature that we see a nearly even distribution of male and female hatchlings. At temperatures below this pivotal temperature we see primarily male populations and above this we see primarily female populations. In recent years, inordinate ratios of female to male eggs have been observed, and this trend could lead to the extinction of sea turtles [12, 14].

Female sea turtles often return to the beaches where they were born to lay their eggs. They dig their nests in the sand, which leads us to investigate the factors that act on the sand temperatures as major impacts on the sex ratios of the hatchlings. This is the focus of many biologists [13][5][7][11]. One hypothesis is that climate change will lead to increased sand temperatures, which is due to the relationship between air temperatures and sand temperatures [6]. Naturally, this hypothesis leads us to question the overall impacts of climate change on the ratios of male and female sea turtles that will lead to extinction.

2 Mathematical Background

In this paper, we use a system of ordinary differential equations (ODEs) constructed by Herrera et al. to model the population sex demographics of green sea turtles. [8]. This capstone paper addresses the same questions that Herrera et al. [8] propose about the impacts of climate change on TSD and the sex ratios that will eventually lead to extinction of green sea turtles. The following investigation introduces the model created in the previous study [8], finds the equilibrium points, analyzes the stability of the non-zero equilibrium point, a step that was not included by Herrera et al., and proposes methods for follow-up studies.

Prior to the mathematical analysis, it is imperative that vocabulary is explained. An equilibrium point is any point, y_0, where $\frac{dy}{dt} = f(y) = 0$. Equilibrium points can be classified into three categories: a sink, a source, or a node. A sink is where any solution with an initial condition sufficiently close to y_0 asymptotically approaches y_0 as t increases. A source is where all solutions that start sufficiently close to y_0 tend toward y_0 as t decreases. A node is neither a sink nor a source. A sink is a point that attracts certain solutions or they approach the point, while a source repels solutions or they leave that point. In a single ODE, by definition, the point $\boldsymbol{Y}_0$ is an equilibrium point for the system $\frac{d\boldsymbol{Y}}{dt} = F(\boldsymbol{Y})$ if $F(\boldsymbol{Y}_0) = 0$. The constant function $\boldsymbol{Y}(t) = \boldsymbol{Y}_0$ is an equilibrium solution [3]. In the system discussed in this capstone, we will be working with multiple ODEs with multiple variables.

Additionally, we discuss the finding of eigenvalues. Given a matrix A, a number λ is called an eigenvalue of A if there is a non-zero vector $\boldsymbol{V} = (x, y, ..., n)$ for which $A\boldsymbol{V} = A\begin{pmatrix} x \\ y \\ ... \\ n \end{pmatrix} = \lambda \begin{pmatrix} x \\ y \\ ... \\ n \end{pmatrix} = \lambda\boldsymbol{V}$. The vector $\boldsymbol{V}$ is called an eigenvector corresponding to the eigenvalue λ. To find the eigenvalues of the matrix A, we must find the values of λ for which $det(A - \lambda I) = 0$. In the case where there are n distinct real eigenvalues $\lambda_1, \lambda_2, ..., \lambda_n$, the general solution is $\boldsymbol{Y}(t) = C_1 k_1 e^{\lambda_1 t} + C_2 k_2 e^{\lambda_2 t} + ... + C_n k_n e^{\lambda_n t}$. When $\lambda_1, \lambda_2, ..., \lambda_n$ are all negative, this equilibrium point is considered to be asymptotically stable, or a sink [9]. If any $\lambda_1, \lambda_2, ..., \lambda_n$ are positive, then the equilibrium point is unstable, either a source or a node [9]. These terms- sink, source, and node- have been used in 2x2 systems [3], but it is unclear if they are used for larger NxN systems. From this point we refer to them as stable or unstable equilibrium points

Suppose that $Y\left(t\right)$ is a complex-valued solution to a linear system

$$\frac{dY}{dt} = AY = \begin{pmatrix} a & b \\ c & d \end{pmatrix} Y,$$

where the coefficient matrix A has all real entries. The determinant equation above might have real and complex solutions, so that means that we may end up with complex exponents. Suppose $Y\left(t\right) = Y_{re}\left(t\right) + iY_{im}\left(t\right)$, where $Y_{re}\left(t\right)$ and $Y_{im}\left(t\right)$ are real valued functions of t. Then $Y_{re}\left(t\right)$ and $Y_{im}\left(t\right)$ are both solutions of the original system $\frac{dY}{dt} = AY$ [3]. Given a linear system with complex eigenvalues of the form $\lambda = \alpha \pm i\beta, \beta > 0$, the solution curves spiral around the origin in the phase plane. Moreover, if α is negative, then the solution is a spiral sink. If α is positive, then the solution is a spiral source. And, if $\alpha = 0$ then the solution is called a center [3].

In this paper, we investigate non-linear systems of differential equations. In order to look at the linear portion of these equations, we can use calculus to calculate the tangent plane. This is considered to be the best linear approximation of the nonlinear right-hand side of the ODE system. The reason for finding the linear portion is because we have solution techniques and analysis for linear systems, while non-linear systems are too difficult to manipulate by hand. This matrix of partial derivatives in this expression is called the *Jacobian Matrix*, J. The Jacobian matrix extracts the linear component of the nonlinear system so we can perform analysis on hte easier-to-handle linear equations. In other words, we can use this linearized system to study the behavior of solutions of the nonlinear system near the equilibrium point. If all eigenvalues of the Jacobian Matrix are negative real numbers or complex number with negative real parts, then the equilibrium point it is asymptotically stable. If the opposite is the case, then it is unstable.

It is important to note that in this paper we use a 4x4 matrix in the form

$$\begin{bmatrix} a & b & c & d \\ e & f & g & h \\ i & j & k & l \\ m & n & o & p \end{bmatrix}.$$

To find the determinant of a 4x4 matrix, we can write $A - \lambda I$ as

$$\begin{bmatrix} a-\lambda & b & c & d \\ e & f-\lambda & g & h \\ i & j & k-\lambda & l \\ m & n & o & p-\lambda \end{bmatrix}.$$

and $det\,(A - \lambda I)$ as

$$(a-\lambda) * det \begin{pmatrix} f-\lambda & g & h \\ j & k-\lambda & l \\ n & o & p-\lambda \end{pmatrix} - b * det \begin{pmatrix} e & g & h \\ i & k-\lambda & l \\ m & o & p-\lambda \end{pmatrix}$$

$$+c * det \begin{pmatrix} e & f-\lambda & h \\ i & j & l \\ m & n & p-\lambda \end{pmatrix} - d * det \begin{pmatrix} e & f-\lambda & g \\ i & j & k-\lambda \\ m & n & o \end{pmatrix}.$$

We can then expand this to be

$$(a-\lambda)\left[(f-\lambda) * det \begin{pmatrix} k-\lambda & l \\ o & p-\lambda \end{pmatrix} - g * det \begin{pmatrix} j & l \\ n & p-\lambda \end{pmatrix} + h * det \begin{pmatrix} j & k-\lambda \\ n & o \end{pmatrix}\right]$$

$$-b\left[e * det \begin{pmatrix} k-\lambda & l \\ o & p-\lambda \end{pmatrix} - g * det \begin{pmatrix} i & l \\ m & p-\lambda \end{pmatrix} + h * det \begin{pmatrix} i & k-\lambda \\ m & o \end{pmatrix}\right]$$

$$+c\left[e * det \begin{pmatrix} j & l \\ n & p-\lambda \end{pmatrix} - (f-\lambda) * det \begin{pmatrix} i & l \\ m & p-\lambda \end{pmatrix} + h * det \begin{pmatrix} i & j \\ m & n \end{pmatrix}\right]$$

$$-d\left[e * det \begin{pmatrix} j & k-\lambda \\ n & o \end{pmatrix} - (f-\lambda) * det \begin{pmatrix} i & k-\lambda \\ m & o \end{pmatrix} + g * det \begin{pmatrix} i & j \\ m & n \end{pmatrix}\right].$$

Finally, we expand this as:

$$(a-\lambda)\left[(f-\lambda)\left[(k-\lambda)(p-\lambda)-(o)(l)\right]-g[(j)(p-\lambda)-(n)(l)]+h[(j)(o)-(k-\lambda)(n)]\right]$$

$$-b[e[(k-\lambda)(p-\lambda)-(o)(l)]-g[(i)(p-\lambda)-(m)(l)]+h[(i)(o)-(k-\lambda)(m)]]$$

$$+c[e[(j)(p-\lambda)-(n)(l)]-(f-\lambda)\left[(i)(p-\lambda)-(m)(l)\right]+h[(i)(n)-(m)(j)]]$$

$$-d[e[(j)(o)-(n)(k-\lambda)]-(f-\lambda)\left[(i)(o)-(m)(k-\lambda)\right]+g[(i)(n)-(m)(j)]].$$

We can then set this equation equal to zero and solve for the eigenvalues of this system.

3 Mathematical Analysis and Results

The mathematical analysis begins with given equations from Herrera et al. [8]. The description and units for the parameters are included in Table 1 where all values are provided by Herrera et al. [8] unless otherwise noted.

$$\frac{dA_M}{dt} = \alpha_M E_M - \mu_M A_M, \tag{1}$$

$$\frac{dA_F}{dt} = \alpha_F E_F - \mu_F A_F, \tag{2}$$

$$\frac{dE_M}{dt} = -\alpha_M E_M + pr\left(1 - \frac{A_M + A_F}{K}\right)\left(\frac{b\frac{A_F}{A_M}}{\frac{A_F}{A_M} + a}\right)A_M - \mu_E E_M, \tag{3}$$

$$\frac{dE_F}{dt} = -\alpha_F E_F + (1-p)\,r\left(1 - \frac{A_M + A_F}{K}\right)\left(\frac{b\frac{A_F}{A_M}}{\frac{A_F}{A_M} + a}\right)A_M - \mu_E E_F \tag{4}$$

Parameter	Description	Estimates
α_M	Maturity rate of eggs that become adult males	$0.022 \pm 0.004yr^{-1}$
α_F	Maturity rate of eggs that become adult females	$0.029 \pm 0.05yr^{-1}$
μ_m	Leaving rate of adult males	$0.05 \pm 0.09yr^{-1}$
μ_F	Leaving rate of adult females	$0.04 \pm 0.07yr^{-1}$
μ_E	Death rate for eggs	$0.36 \pm 0.33yr^{-1}$
p	Proportion of eggs that become male	N/A
r	Average number of eggs per successful interaction	117 ± 38
b	Interaction rate	$180 \pm 20yr^{-1}$
a	Half saturation constant, equal to $\frac{b}{c}$	90 [1]
K	Carrying capacity of adults	73600 [4]

Parameter descriptions and values from [8]

3.1 Model Description

The development of this model comes from the life cycle of green sea turtles. Their life starts when they emerge from their shells and travel to the ocean. The turtles remain at sea during their juvenile stage and often don't reappear for several years. The turtles reach sexual maturity between 40-60 years of age [8], and they return to their natal beaches to mate or nest. Male turtles commonly mate every two years while females lay eggs every 2-5 years [10]. Sea turtles are able to have multiple mates and lay several clutches each breeding season. These eggs will then develop into male or female turtles depending on the incubation temperature. It is also important to note that the death of adult turtles, as well as movement out of reproductive stages, decrease the adult population, while the death of eggs and juveniles reduced the population of the "eggs" class [8]. This information was used to create the model of the simplified life cycle seen in Figure 1.

This model also uses many parameters including the density of the female population, the density of the male population, behavioral responses of females

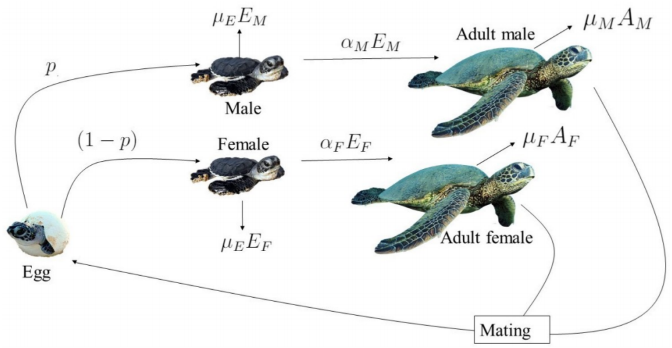

Figure 1: Schematic diagram of the mathematical model [8]

during mating, and characteristics of males such as searching efficiency. Following Herrera et al. [8] we limit our attention to the proportions of eggs that are male and female. The population is divided into two groups: adults and eggs, where adults refers to those in reproductive stages and eggs are those in pre-reproductive stages. The egg population and adult population for males and females are denoted as $E_M(t)$, $E_F(t)$, $A_M(t)$, and $A_F(t)$, respectively, and are functions of time t.

The first two differential equations, Equations (1) and (2), in the system below represent the total number of eggs that will reach adulthood denoted by $\alpha_M E_M$ for males and $\alpha_M E_F$ for females. They also show the total number of adults that leave the sexually reproductive stage denoted by $\mu_M A_M$ for males and $\mu_F A_F$ for females. The second two differential equations, Equations (3) and (4) show the flow of turtles leaving the egg stage and entering the sexually reproductive stage. These equations tell us the rates at which turtles are entering the population and the rate at which some leave, whether that be by aging out or death.

The total number of male eggs and female eggs produced per successful interaction per unit of time is represented as $\frac{b\frac{A_F}{A_M}}{\frac{A_F}{A_M}+a}A_M$. The average number of eggs in a clutch is represented by r, the proportion of male or female eggs are represented by p and $1-p$ respectively, and the saturation constraint is represented by $1-\frac{A_M+A_F}{K}$ where K is the carrying capacity.

The parameters α_M and α_F are maturity rates that show the number of male and female hatchlings that survive onto the reproductive stage, while μ_M and μ_F show the leaving rates of reproductive males and females, which include death of sexually mature turtles and the rate at which adults move to the post-reproductive stages. The variable μ_E is the death rate of turtles in the egg and juvenile stages. The duration of courtship and copulation is indicated by t_h, or handling time, and the searching efficiency is defined as c, which is the rate at which a male finds a female. The copulation rate is denoted by $b = \frac{1}{t_h}$ and the half saturation constant is $a = \frac{1}{ct_h}$.

3.2 Finding A Non-Zero Equilibrium Point

First, it is important to note that there is a zero equilibrium point. This is the point where all four variables are zero, then the right-hand sides of all four equations will be zero as well. Herrera et al. find this point to be asymptotically attractive if the birth rate minus the mortality of eggs is less than zero ($rb - \mu < 0$) which means that the turtle population would go extinct.

Recall that to find the non-zero equilibrium points we must set the differential equation equal to 0. In doing so for each equation, we see that Equation (1) becomes

$$\alpha_M E_M - \mu_M A_M = 0 \implies \alpha_M E_M = \mu_M A_M, \tag{5}$$

Equation (2) becomes

$$\alpha_F E_F - \mu_F A_F = 0 \implies \alpha_F E_F = \mu_F A_F \, (2b) \, , \tag{6}$$

Equation (3) can be written as

$$-\alpha_M E_M + pr\left(1 - \frac{A_M + A_F}{K}\right)\left(\frac{b\frac{A_F}{A_M}}{\frac{A_F}{A_M} + a}\right) A_M - \mu_E E_M = 0 \tag{7}$$

$$\implies pr\left(1 - \frac{A_M + A_F}{K}\right)\left(\frac{b\frac{A_F}{A_M}}{\frac{A_F}{A_M} + a}\right) A_M = \alpha_M E_M + \mu_E E_M, \tag{8}$$

and lastly, Equation (4) can be written as

$$-\alpha_F E_F + (1-p)\, r\left(1 - \frac{A_M + A_F}{K}\right)\left(\frac{b\frac{A_F}{A_M}}{\frac{A_F}{A_M} + a}\right) A_M - \mu_E E_F = 0 \tag{9}$$

$$\implies pr\left(1 - \frac{A_M + A_F}{K}\right)\left(\frac{b\frac{A_F}{A_M}}{\frac{A_F}{A_M} + a}\right) A_M = \alpha_F E_F + \mu_E E_F. \tag{10}$$

We can then add the four equations (5, 6, 8, and 10) to get

$$\alpha_M E_M + \alpha_F E_F + pr\left(1 - \frac{A_M + A_F}{K}\right)\left(\frac{b\frac{A_F}{A_M}}{\frac{A_F}{A_M} + a}\right) A_M + (1-p)\, r\left(1 - \frac{A_M + A_F}{K}\right)\left(\frac{b\frac{A_F}{A_M}}{\frac{A_F}{A_M} + a}\right) A_M$$

$$= \mu_M A_M + \mu_F A_F + (\alpha_M EM + \mu_E E_M) + (\alpha_F E_F + \mu_E E_F)$$

and by simplifying we obtain the equation

$$r\left(1 - \frac{A_M + A_F}{K}\right)\left(\frac{b\frac{A_F}{A_M}}{\frac{A_F}{A_M} + a}\right) A_M = \mu_M A_M + \mu_F A_F + \mu_E E_M + \mu_E E_F. \tag{11}$$

From Equations (5) and (6), we know

$$E_M = \frac{\mu_M}{\alpha_M} A_M, E_F = \frac{\mu_F}{\alpha_F} A_F. \tag{12}$$

By substituting Equation (12) into Equation (11), we obtain

$$r\left(1 - \frac{A_M + A_F}{K}\right)\left(\frac{b\frac{A_F}{A_M}}{\frac{A_F}{A_M} + a}\right) A_M = \mu_M A_M + \mu_F A_F + \mu_E\left(\frac{\mu_M A_M}{\alpha_M}\right) + \mu_E\left(\frac{\mu_F A_F}{\alpha_F}\right)$$

We can then multiply μ_E into the numerator of each fraction to obtain

$$\mu_M A_M + \mu_F A_F + \frac{\mu_E \mu_M A_M}{\alpha_M} + \frac{\mu_E \mu_F A_F}{\alpha_F}$$

We then pull out the A_M and A_F and rearrange the equation

$$\mu_M A_M + \frac{\mu_E \mu_M}{\alpha_M} A_M + \mu_F A_F + \frac{\mu_E \mu_F}{\alpha_F} A_F$$

by pulling out the A_M and A_F we get

$$A_M\left(\mu_M + \frac{\mu_E \mu_M}{\alpha_M}\right) + A_F\left(\mu_F + \frac{\mu_E \mu_F}{\alpha_F}\right)$$

Finally, we can multiply μ_M by $\frac{\alpha_M}{\alpha_M}$ and multiply μ_F by $\frac{\alpha_F}{\alpha_F}$ and combine the fractions.

$$A_M \frac{\alpha_M \mu_M + \mu_E \mu_M}{\alpha_M} + A_F \frac{\alpha_F \mu_F + \mu_E \mu_F}{\alpha_F}.$$

We then can rewrite equation (10) as

$$r\left(1 - \frac{A_M + A_F}{K}\right)\left(\frac{b\frac{A_F}{A_M}}{\frac{A_F}{A_M} + a}\right) A_M = \frac{(\alpha_M + \mu_E)}{p} E_M \tag{13}$$

and substituting Equation (12) into Equation (13) we get

$$r\left(1 - \frac{A_M + A_F}{K}\right)\left(\frac{b\frac{A_F}{A_M}}{\frac{A_F}{A_M} + a}\right) A_M = \frac{(\mu_E + \alpha_M)\,\mu_M}{\alpha_M p} A_M. \tag{14}$$

Using equations (11) and (14) we obtain

$$\frac{\alpha_M \mu_M + \mu_M \mu_E}{\alpha_M} A_M + \frac{\alpha_F \mu_F + \mu_F \mu_E}{\alpha_F} A_F = \frac{(\mu_E + \alpha_M)\,\mu_M}{\alpha_M p} A_M. \tag{15}$$

We can rewrite Equation (15) to obtain a relationship between A_M and A_F: $HA_M = GA_F$ where $\frac{A_M}{A_F} = \frac{H}{G}$ and $A_M + A_F = \left(1 + \frac{H}{G}\right) A_M$, and $H = \frac{(1-p)(\mu_E+\alpha_M)\mu_M}{\alpha_M p}$ and $G = -\frac{\alpha_F \mu_F + \mu_F \mu_E}{\alpha_F}$. Using these equations, we can expand Equation (15) to find the equilibrium point. We can rearrange Equation (14) to read as

$$\frac{r}{K}\left(K - (A_M + A_F)\right)\left(\frac{b\frac{A_F}{A_M}}{\frac{A_F}{A_M}}\right) A_M = \frac{(\mu_E + \alpha_M)\mu_M}{\alpha_M p} A_M.$$

We can then plug in using the relationships previously described to get

$$\frac{r}{K}\left(\left(1+\frac{H}{G}\right)A_M\right)\left(\frac{b\frac{H}{G}}{\frac{H}{G}+a}\right)A_M=\frac{\left(\mu_E+\alpha_M\right)\mu_M}{\alpha_M p}A_M.$$

To get rid of the fractionHG within the fraction, we can multiply the left-hand side by $\frac{G}{G}$

$$\frac{r}{K}\left(K-A_M-\frac{HA_M}{G}\right)\left(\frac{bH}{H+Ga}\right)A_M=\frac{\left(\mu_E+\alpha_M\right)\mu_M}{\alpha_M}A_M.$$

We then multiply through $\frac{r}{K}$ to get

$$\left(r-\frac{rA_M}{K}-\frac{rHA_M}{KG}\right)\left(\frac{bH}{H+Ga}\right)A_M=\frac{\left(\mu_E+\alpha_M\right)\mu_M}{\alpha_M p}A_M.$$

Then, we combine the fractions and get the equation

$$\left(\frac{rKG-rGA_M-rHA_M}{KG}\right)\left(\frac{bH}{H+Ga}\right)A_M=\frac{\left(\mu_E+\alpha_M\right)\mu_M}{\alpha_M p}A_M.$$

Because each term has an r, we can pull that out in the numerator. We can also cancel the A_M term on both sides.

$$\frac{r\,(kG-GA_M-HA_M}{KG}\left(\frac{bH}{H+Ga}\right)=\frac{\left(\mu_E+\alpha_M\right)\mu_M}{\alpha_M p}$$

We then can group and pull out the A_M in the numerator in the left-hand side.

$$\frac{r\left(KG-\left(H+G\right)A_M\right)}{KG}\left(\frac{bH}{H+Ga}\right)=\frac{\left(\mu_E+\alpha_M\right)\mu_M}{\alpha_M p}$$

We then multiply the two factions on the left-hand side together to get

$$\frac{bHr\left(KG-\left(H+G\right)A_M\right)}{KG\left(H+Ga\right)}=\frac{\left(\mu_E+\alpha_M\right)\mu_M}{\alpha_M p}$$

We then multiply the right-hand side by the denominator of the left-hand side and multiply the left-hand side by the denominator from the right-hand side.

$$\alpha_M pbHr\left(KG-\left(H+G\right)A_M\right)=\left(\mu_E+\alpha_M\right)\mu_M KG\left(H+Ga\right)$$

Through multiplication and rearranging the equation we get

$$KG\alpha_M pbHr-\left(H+G\right)A_M\alpha_M pbHr=\left(\mu_E+\alpha_M\right)\mu_M\left(H+Ga\right)KG\implies$$

$$KG\alpha_M pbHr-\left(\mu_E+\alpha_M\right)\mu_M\left(H+Ga\right)=\left(H+G\right)A_M\alpha_M pbHr.$$

We can then divide both sides by $\alpha_M pbHr$ to get

$$KG-\frac{\left(\mu_E+\alpha_M\right)\mu_M\left(H+Ga\right)KG}{\alpha_M pbHr}=\left(H+G\right)A_M$$

We can then pull out a G from each term on the left-hand side:

$$G\left(K-\frac{(\mu_E+\alpha_M)\,\mu_M\,(H+Ga)\,K}{\alpha_M pbHr}\right)=(H+G)\,A_M$$

We then divide by $(H+G)$

$$\frac{G\left(K-\frac{(\mu_E+\alpha_M)\mu_M(H+Ga)K}{\alpha_M pbHr}\right)}{H+G}=A_M^*.$$

We can then write $A_M^*=\frac{(K-Q)G}{H+G}$ where $Q=\frac{(\mu_E+\alpha_M)\mu_M(H+aG)K}{\alpha_M pbHr}$. Using the relationship between A_M, A_F, E_M, and E_F, we can find the equilibrium point, I^*.

$$I^*=\left(A_M^*,\frac{H}{G}A_M^*,\frac{\mu_M}{\alpha_M}A_M^*,\frac{H\mu_F}{G\alpha_F}A_M^*\right).$$

Now that a non-zero equilibrium point has been found, we can determine if it is a stable or unstable point.

3.3 Stability of the Equilibrium Point

As previously mentioned, to determine the stability of the equilibrium point we must first find the eigenvalues that correspond to the system of equations. We mist first find the Jacobian matrix by taking the partial derivatives of the system. Let f_i denote the right hand side of Equation (i) for $i=1,2,3,4$. Then

$$\begin{aligned}
\frac{\partial f_1}{\partial A_M} &= -\mu_M,\\
\frac{\partial f_1}{\partial A_F} &= 0,\\
\frac{\partial f_1}{\partial E_M} &= \alpha_M,\\
\frac{\partial f_1}{\partial E_F} &= 0.
\end{aligned}$$

$$\begin{aligned}
\frac{\partial f_2}{\partial A_M} &= 0,\\
\frac{\partial f_2}{\partial A_F} &= -\mu_F,\\
\frac{\partial f_2}{\partial E_M} &= 0,\\
\frac{\partial f_2}{\partial E_F} &= \alpha_F.
\end{aligned}$$

$$\frac{\partial f_3}{\partial A_M} = pr\left(A_M-\frac{1}{K}A_M^2+\frac{1}{K}A_FA_M\right)\left(\frac{abA_F}{(A_F+aA_M)^2}\right)+\frac{bA_F}{A_F+aA_M}pr\left(1-\frac{2}{K}A_M+\frac{A_F}{K}\right),$$

(17)

$$\begin{aligned}
\frac{\partial f_3}{\partial A_F} &= pr\left(A_M - \frac{1}{K}A_M^2 + \frac{1}{K}A_F A_M\right)\left(\frac{A_F + abA_M - bA_F}{(A_F + aA_M)^2}\right) + pr\left(\frac{1}{K}A_M\right)\left(\frac{bA_F}{A_F + aA_M}\right), \\
\frac{\partial f_3}{\partial E_M} &= -\alpha_M - \mu_E, \\
\frac{\partial f_3}{\partial E_F} &= 0.
\end{aligned}$$

$$\frac{\partial f_4}{\partial A_M} = (1-p)\,r\left(A_M - \frac{1}{K}A_M^2 + \frac{1}{K}A_F A_M\right)\left(\frac{abA_F}{(A_F + aA_M)^2}\right) + \frac{bA_F}{A_F + aA_M}(1-p)\,r\left(1 - \frac{2}{K}A_M + \frac{A_F}{K}\right),$$

(19)

$$\begin{aligned}
\frac{\partial f_4}{\partial A_F} &= (1-p)\,r\left(A_M - \frac{1}{K}A_M^2 + \frac{1}{K}A_F A_M\right)\left(\frac{A_F + abA_M - bA_F}{(A_F + aA_M)^2}\right) + (1-p)\,r\left(\frac{1}{K}A_M\right)\left(\frac{bA_F}{A_F + aA_M}\right), \\
\frac{\partial f_4}{\partial E_M} &= 0, \\
\frac{\partial f_4}{\partial E_F} &= -\alpha_F - \mu_F.
\end{aligned}$$

Now, we have the Jacobian Matrix for the system.

$$\begin{bmatrix}
-\mu_M & - \\
0 & \\
pr\left(A_M - \frac{1}{K}A_M^2 + \frac{1}{K}A_F A_M\right)\left(\frac{abA_F}{(A_F+aA_M)^2}\right) + \frac{bA_F}{A_F+aA_M}pr\left(1 - \frac{2}{K}A_M + \frac{A_F}{K}\right) & pr\left(A_M - \frac{1}{K}A_M^2 + \frac{1}{K}A_F A_M\right)\left(\frac{A_F+a}{(A_F}\right. \\
(1-p)\,r\left(A_M - \frac{1}{K}A_M^2 + \frac{1}{K}A_F A_M\right)\left(\frac{abA_F}{(A_F+aA_M)^2}\right) + \frac{bA_F}{A_F+aA_M}(1-p)\,r\left(1 - \frac{2}{K}A_M + \frac{A_F}{K}\right) & (1-p)\,r\left(A_M - \frac{1}{K}A_M^2 + \frac{1}{K}A_F A_M\right)\left(\frac{A_F+a}{(A_F}\right.
\end{bmatrix}$$

For each of the equations $\frac{\partial\frac{dE_M}{dt}}{dA_M}$, $\frac{\partial\frac{dE_F}{dt}}{dA_M}$, $\frac{\partial\frac{dE_M}{dt}}{dA_F}$, and $\frac{\partial\frac{dE_F}{dt}}{dA_F}$ we can plug in the equilibrium solutions. In doing so we can follow that

$$\frac{\partial\frac{dE_M}{dt}}{dA_M} = pr\left(\left(A_M - \frac{A_M^2}{K} + \frac{\frac{H}{G}A_M^2}{K}\right)\left(\frac{ab\frac{H}{G}A_M}{\left(\frac{H}{G}+a\right)A_M}\right) + \left(\frac{\frac{bH}{G}A_M}{\left(\frac{H}{G}+a\right)A_M}\right)\left(1 - \frac{2A_M}{K} + \frac{\frac{H}{G}A_M}{K}\right)\right) \implies$$

$$pr\left(\frac{KA_M - A_M^2 + \frac{H}{G}A_M^2}{K}\right)\left(\frac{ab\frac{H}{G}}{\left(\frac{H}{G}+a\right)}\right) + \left(\frac{\frac{bH}{G}}{\left(\frac{H}{G}+a\right)}\right)\left(\frac{K - 2A_M + \frac{H}{G}A_M}{K}\right) \implies$$

$$pr\left(\frac{ab\frac{H}{G}\left(KA_M - A_M^2 + \frac{H}{G}A_M^2\right) + \frac{bH}{G}\left(K - 2A_M + \frac{H}{G}A_M\right)}{K\left(\frac{H}{G}+a\right)}\right) \implies$$

$$pr\frac{bH}{G}\left(\frac{a\left(KA_M - A_M^2 + \frac{H}{G}A_M^2\right) + K - 2A_M + \frac{H}{G}A_M}{K\left(\frac{H}{G}+a\right)}\right) \implies$$

$$prbH\left(\frac{aKA_M - aA_M^2 + a\frac{H}{G}A_M^2 + K - 2A_M + \frac{H}{G}A_M}{K\left(\frac{H}{G}+a\right)}\right)$$

finally we can multiply by G to get

$$prbH\left(\frac{aKA_MG-aA_M^2G+HaA_M^2+HA_M+KG-2A_MG}{K\left(H+aG\right)}\right).$$

When we plug in the equilibrium solutions to

$$\frac{\partial\frac{dE_M}{dt}}{dA_F}=pr\left(A_M-\frac{A_M^2}{K}+\frac{A_FA_M}{K}\right)\left(\frac{A_F+abA_M-bA_F}{\left(A_F+aA_M\right)^2}\right)+pr\left(\frac{A_M}{K}\right)\left(\frac{bA_F}{A_F+aA_M}\right)\implies$$

$$pr\left(\left(A_M-\frac{A_M^2}{K}+\frac{A_FA_M}{K}\right)\left(\frac{A_F+abA_M-bA_F}{\left(A_F=aA_M\right)^2}\right)+\left(\frac{bA_FA_M}{K\left(A_F+aA_M\right)}\right)\right)\implies$$

$$pr\left(\left(\frac{KA_M-A_M^2+\frac{H}{G}A_M^2}{K}*\frac{\frac{H}{G}A_M+abA_M-b\frac{H}{G}A_M}{\left(\frac{H}{G}A_M+aA_M\right)^2}\right)+\frac{b\frac{H}{G}A_M^2}{K\left(\frac{H}{G}A_M+aA_M\right)}\right)\implies$$

$$pr\left(\frac{A_M\left(K-A_M+\frac{H}{G}A_M\right)}{K}*\frac{A_M\left(\frac{H}{G}+ab-\frac{bh}{G}\right)}{A_M\left(\frac{H}{G}+a\right)^2}\right)+\frac{b\frac{H}{G}A_M^2}{KA_M\left(\frac{H}{G}+a\right)}\implies$$

$$pr\left(\frac{A_M^2\left(K-A_M+\frac{H}{G}A_M\right)\left(\frac{H}{G}+ab-\frac{bH}{G}\right)}{A_M^2\left(\frac{H}{G}+a\right)^2}\right)+\frac{b\frac{H}{G}A_M}{K\left(\frac{H}{G}+a\right)}\implies$$

$$pr\left(\frac{\left(K-A_M+\frac{H}{G}A_M\right)\left(\frac{H}{G}+ab-\frac{bH}{G}\right)}{\left(\frac{H}{G}+a\right)^2}\right)+\frac{b\frac{H}{G}A_M}{K\left(\frac{H}{G}+a\right)}\implies$$

$$\frac{pr\left(K\left(A_MH-A_MG+KG\right)\left(H-Hb+Gab\right)+A_MHb\left(H+Ga\right)\right)}{K\left(H+aG\right)}.$$

When we plug in the equilibrium solutions for

$$\frac{\partial\frac{dE_F}{dt}}{dA_M}=\left(1-p\right)r\left(A_M-\frac{A_M^2}{K}+\frac{A_FA_M}{K}\right)\left(\frac{abA_F}{\left(A_F+aA_M\right)^2}\right)+\frac{bA_F}{A_F+aA_M}\left(1-p\right)r\left(1-\frac{2A_M}{K}+\frac{A_M}{K}\right)$$

we obtain

$$\left(1-p\right)rbH\left(\frac{A_M\left(aK-2+\frac{H}{G}\right)-aA_M^2\left(1+\frac{H}{G}\right)+K}{K\left(\frac{H}{G}+a\right)}\right)$$

which leads us to

$$\frac{\left(1-p\right)rbH\left(aKA_MG-aA_M^2G+HaA_M^2+A_M-KG-2A_MG\right)}{K\left(H+aG\right)}.$$

Lastly, if we plug the equilibrium solutions into

$$\frac{\partial\frac{dE_F}{dt}}{dA_F}=\left(1-p\right)r\left(A_M-\frac{A_M^2}{K}+\frac{A_FA_M}{K}\right)\left(\frac{A_F+abA_M-bA_F}{\left(A_F+aA_M\right)^2}\right)+\left(1-p\right)r\left(\frac{A_M}{K}\right)\left(\frac{bA_F}{A_F+aA_M}\right)$$

we get

$$(1-p)\,r\left(\frac{\left(K-A_M+\frac{H}{G}A_M\right)\left(\frac{H}{G}+ab-\frac{bH}{G}\right)}{\frac{H}{G}+a^2}+\frac{b\frac{H}{G}A_M}{K\left(\frac{H}{G}+a\right)}\right).$$

We can then combine the fractions to obtain

$$\frac{(1-p_r\left(A_MH-A_MG+KG\right)\left(H-Hb+Gab\right)+A_MHb\left(H+Ga\right)}{K\left(H+Ga\right)^2}.$$

Now that we have solved for each of these partial derivatives at the equilibrium points, we are able to find the values for the Jacobian matrix to determine the eigenvalues for the system. As noted earlier, $H=\frac{(1-p)(\mu_E+\alpha_M)\mu_M}{\alpha_M p}$ and $G=-\frac{\alpha_F\mu_F+\mu_F\mu_E}{\alpha_F}$ and $Q=\frac{(\mu_E+\alpha_M)\mu_M(H+aG)K}{\alpha_M pbHr}$. To find the values of the Jacobian Matrix, we use the mean values from Table 1. The variable p is not fixed, meaning that it can be a different constant in different situations, and we can adjust it to see the effects that different sex ratios have on the stability of the system. For the purpose of this paper we investigate the system using $p=0.1$. This value says that ten percent of the population born becomes males. This follows from research from NOAA [1] that states that 85%-95% of turtles become female.

After plugging in the variables, we find

$$J=\begin{bmatrix}-0.05-\lambda & 0 & 0.022 & 0\\ 0 & -0.04-\lambda & 0 & 0.029\\ -1.24816*10^8 & 2.0009*10^6 & -0.382-\lambda & 0\\ -1.12334*10^9 & 1.80081*10^7 & 0 & -0.389-\lambda\end{bmatrix}.$$

We can then take the determinant of this matrix as explained earlier. In doing so we get

$$(-0.05-\lambda)\left[(-0.04-\lambda)\left((-0.382-\lambda)(-0.389-\lambda)\right)+(0.029)\left(\left(2.0009*10^6\right)(-0.389-\lambda)\right.\right.$$
$$\left.-\left(1.80081*10^7\right)(-0.382-\lambda)\right]+(0.022)\left[-(-0.004-\lambda)\left(\left(-1.24816*10^7\right)(-0.389-\lambda)-\right.\right.$$
$$\left(-1.12334*10^7\right)(0)+(0.029)\left(\left(-1.24816*10^7\right)\left(1.80081*10^7\right)-\right.$$
$$\left(-1.12334*10^7\right)\left(2.0009*10^6\right)\Big]=0$$

Then, when we multiply this out, we get

$$(0.05-\lambda)\left[(-0.04-\lambda)\left[(0.148598)+0.771\lambda+\lambda^2\right]\right]+\left[(0.029)\left[(-778350.1)-2000900\lambda+6879094.2\right.\right.$$
$$\left.\left.+18008100\lambda\right]\right]+\left[(0.022)\left[\left[(0.04+\lambda)(4855342.4+12481600\lambda)\right]\right]+\left[(0.029)\left[\left(-2.24769901*10^{14}\right)\right.\right.\right.$$
$$\left.\left.\left.+\left(2.247691006*10^{13}\right)\right]\right]\right]=0.$$

Simplifying this out further, we find

$$(0.05-\lambda)\left[176921.5734+464208.6206\lambda-0.811\lambda^2-\lambda^3\right]$$

$$+[-1.29062924 * 10^{11} + 117801.3408\lambda + 274595.2\lambda^2] = 0.$$

And, finally we find the polynomial

$$-1.29062915 * 10^{11} - 35909.80157\lambda - 189613.4612\lambda^2 + 0.761\lambda^3 + \lambda^4 = 0$$

Finally, I was able to use Mathematica to calculate the roots of the polynomial. The eigenvalues for this system with these parameters are $\lambda_1 = -683.12, \lambda_2 = 682.69, \lambda_3 = -0.165867 - 526.066i$, and $\lambda_4 = -0.165867 + 526.066i$.

I also chose to investigate the effect of the clutch size on the system. Using the minimum number given so $r = 79$, I was able to find the eigenvalues to be $\lambda_1 = -403.545, \lambda_2 = 0.790654, \lambda_3 = 201.718 - 1407.74i$, and $\lambda_4 = 201.718 + 1407.74i$. When $r = 155$, $\lambda_1 = -2.09757, \lambda_2 = 1.66861, \lambda_3 = -0.216019 - 1717.47i$ and $\lambda_4 = -0.216091 + 1717.47i$. Looking at these different variations in parameters is important because the numbers are changing rapidly as the environment changes. In this case, changing the values of r would indicate that turtles either laid more eggs than they do at this current moment, or that they lay fewer eggs than they do at this time. Varying the parameters may also provide insight into situations where the nonzero equilibrium point might be stable.

3.4 Poincare-Perron Theorem and Proof

According to the Poincare-Perron Theorem stated by Dr. Howard from Texas A&M [9]: For any ODE System $\frac{d\overrightarrow{y}}{dt}$, suppose $\overrightarrow{y}_e$ denotes an equilibrium point and that $\overrightarrow{f}$ is twice continuously differentiable for $\overrightarrow{y}$ in a neighborhood of $\overrightarrow{y}_e$. (I.e. all second order partial derivatives of each component of $\overrightarrow{f}$ are continuous.) Then $\overrightarrow{y}_e$ is stable or unstable as follows:

1. If the eigenvalues of $\overrightarrow{f'}(\overrightarrow{y}_e)$ all have negative real part, then $\overrightarrow{y}_e$ is asymptotically stable.

2. If any of the eigenvalues of $\overrightarrow{f'}(\overrightarrow{y}_e)$ has positive real part then $\overrightarrow{y}_e$ is unstable.

To provide a proof for Part 1 of the Poincare-Perron Theorem we begin with the equation $\overrightarrow{y} = \overrightarrow{f}(\overrightarrow{y})$, for which $\overrightarrow{y}_e$ is assumed to be an equilibrium point. Under our assumption that $\overrightarrow{f}(\overrightarrow{y}_e)$ is twice continuously differentiable in a neighborhood of $\overrightarrow{y}_e$, we can write the Taylor expansion

$$\overrightarrow{f}(\overrightarrow{y}) = \overrightarrow{f}(\overrightarrow{y}_e) + \overrightarrow{f'}(\overrightarrow{y}_e)(\overrightarrow{y} - \overrightarrow{y}_e) + \overrightarrow{Q}(\overrightarrow{y}, \overrightarrow{y}_e),$$

where we know that $\overrightarrow{f}(\overrightarrow{y}_e) = 0$, $\overrightarrow{Q}$ is a function such that $\overrightarrow{y}$ contained in a radius around the equilibrium point and $|\overrightarrow{Q}(\overrightarrow{y}, \overrightarrow{y}_e)| \leq C|\overrightarrow{y} - \overrightarrow{y}_e|^2$. By setting $\overrightarrow{z} = \overrightarrow{y} - \overrightarrow{y}_e$, we obtain

$$\overrightarrow{z} = \overrightarrow{f}(\overrightarrow{y}_e)\,\overrightarrow{z} + \overrightarrow{Q}(\overrightarrow{y}, \overrightarrow{y}_e),$$

where $|\vec{Q}(\vec{y}_e, \vec{y})| \leq C|\vec{z}|^2$. We can re-write this equation for $\vec{z}$ as

$$\left(e^{-\vec{f}(\to(y)_e}\right) t\vec{z}' = e^{-\vec{f}(\vec{y}_e)(t-s)}\vec{Q}(\vec{y}(s), \vec{y}_e)\, ds.$$

In the first case of the theorem, the eigenvalues of $\vec{f}(\vec{y}_e)$ all have negative real part. If we let λ_R denote the real part of the largest eigenvalues of $\vec{f'}(\vec{y}_e)$, then there exists some constant C_1 so that the largest entry in the matrix $e^{\vec{f'}(\vec{y}_e)(t-s)}$ is bounded in complex modulus by $C_1 e^{\lambda_R t}$. In this way, we see that

$$|\vec{z}(t)| \leq K_1 e^{\lambda_R t}|\vec{z}(0)| + K_2 \int_0^t e^{\lambda_R (t-s)}|\vec{z}(s)|^2 ds \tag{20}$$

where K_1 and K_2 are positive constants. Let $\zeta(t)$ be defined as follows:

$$\zeta(t) := \sup_{a\in|0,t|} |\vec{z}(s)\, e^{-\lambda_R s}|,$$

where *sup* is the supremum. A supremum of a subset of an ordered set is the least element in the set that is greater than or equal to the largest element in the subset. And, note that equation (20) can be rearranged as

$$|\vec{z}(t)\, e^{-\lambda_R t}| \leq K_1|\vec{z}(0)| + K_2 \int_0^t e^{-\lambda_R 2}|\vec{z}(s)|^2 ds.$$

since the right-hand side of equation (20) increases with t, we can take a sup on each side of this last expression to obtain

$$\zeta(t) \leq K_1|\vec{z}(0)| + K_2 \int_0^t e^{-\lambda_R s}|\vec{z}(s)|^2 ds. \leq K_1\zeta(0) + K_2\zeta(t)^2 \int_0^2 e^{\lambda_R s} ds \leq K_1\zeta(0) + \frac{K_2}{|\lambda_R|}\zeta(t)^2. \tag{21}$$

Note especially that since $\zeta(0) = |\vec{z}(0)|$, we are justified in choosing it small as we like. (In the definition of stability, we take $|\vec{z}(0)| \leq \delta$, where δ may be chosen.) The following argument is referred to as *continuous induction.* Since it is important in its own right, we separate it out as a lemma.

Lemma (continuous induction) Suppose there exists a constant C so that

$$\zeta(t) \leq C\left(\zeta(0) + \zeta(t)^2\right), \tag{22}$$

for all $t \geq 0$. If $\zeta(0) < min[1, 1/\left(4C^2\right)]$, then

$$\zeta(t) < 2C\zeta(0), \tag{23}$$

for all $t \geq 0$.

Proof of Lemma We first observe that by (20), and for $\zeta(0) < 1$,

$$\zeta(0) \leq C\left(\zeta(0) + \zeta(0)^2\right) < C(\zeta(0) + \zeta(0)) = 2C\zeta(0),$$

so (22) is satisfied for $t = 0$ and, by continuity for some interval $t \in [0, T]$. Let T, if it exists, denote the first time for which $\zeta(T) = 2C\zeta(0)$. Then

$$\zeta(T) \leq C\left(\zeta(0) + \zeta(T)^2\right) = C\left(\zeta(0) + 4C^2\zeta(0)^2\right) < C(\zeta(0) + \zeta(0)) = 2C\zeta(0),$$

which contradicts the existence of T. IF no such T exists, (21) must be true for all t.

We now conclude our proof of the Poincare-Perron as follows. Let $C = max[K_1, \frac{K_2}{|\lambda_R|}]$. Then by (21), we have

$$\zeta(t) < 2C\zeta(0),$$

or

$$\sup_{s\in[0,t]} |\vec{z}(s)\, e^{-\lambda_R s}| < 2C\zeta(0).$$

In particular,

$$|\vec{z}(t)\, e^{-\lambda_R t}| < 2C\zeta(0),$$

giving at last

$$|\vec{z}(t)| \leq 2C\zeta(0)\, e^{\lambda_R t}.$$

Since $\lambda_R < 0$,

$$\lim_{t\to\infty} |\vec{z}(t)| = \lim_{t\to\infty} 2C\zeta(0)\, e^{\lambda_R t} = 0,$$

which means, according to our definition of asymptotic stability, that $\vec{y}_e$ is asymptotically stable.

At this point, we have found the nonzero equilibrium point and the eigenvalues of the system. After finding the proof to describe asymptotic stability with multiple eigenvalues, we can then turn back to our system with four eigenvalues to determine if the system is asymptotically stable. In the context of turtle populations, this will tell us if the system will go extinct at this equilibrium point or if it will not. We can see that the resulting eigenvalues are not all negative, therefore the equilibrium point is unstable. Then, it takes the form

$$v(t) = c_1 e^{\lambda_1 t}\mathbf{v}_1 + c_2 e^{\lambda_2 t}\mathbf{v}_2 + c_3 Re\left(e^{\lambda_3 t}\mathbf{v}_3\right) + c_4 Im\left(e^{\lambda_4 t}\mathbf{v}_4\right)$$

where $\mathbf{v}_1, \mathbf{v}_2, \mathbf{v}_3$ and $\mathbf{v}_4$ are the corresponding eigenvectors respectively.

4 Conclusion

After completion of this study, there are still questions that must be investigated in the future. The first question would be to investigate the stability of this system using different parameters. What if the proportion of females was higher as suggested by National Geographic [15]. We can also investigate the effects of clutch sizes. As noted above, when $r = 79$ there are three positive eigenvalues and when $r = 155$ there are three negative eigenvalues, but the numbers are closer to zero. It might be useful to use a bifurcation diagram for that study. It would also be of interest to study the number of copulation events that a male turtle would participate in during mating seasons and the current global carrying capacity for sea turtles. Although the paper by Herrera et al. was published in 2019, it would be worth considering more recent data for the parameters provided as time goes on.

For these studies it would be useful to find or create a computer program that would allow all of these parameter changes and eigenvalues to be found. In this study, Mathematica was unable to compute eigenvalues using the unknown parameters in the equations, and once the numbers were found, the program was unable to directly compute the eigenvalues. To biologists, it would be interesting to understand these systems for other species that have different sex determination patterning, different mating rates, or different clutch sizes.

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